The Effect of Ungulate Herbivory on Aspen Communities in South-Central Utah: Measurement of Long-Term Exclosures

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The effect of ungulate herbivory on aspen communities in south-central Utah: Measurement of long-term exclosures.

by

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ABSTRACT

All the aspen exclosures (n=9) on the Dixie and Fishlake National Forests in south-central Utah were measured to determine aspen stem dynamics, successional status, and understory species composition. Several of the exclosures were of a three-part design with a total exclusion portion, a livestock exclusion portion, and a combined use portion, which permitted the effects of deer and elk herbivory to be measured separately from that of livestock, primarily cattle. Aspen within all total exclusion plots successfully regenerated and developed multi-aged stems without fire or other disturbance. Aspen subjected to browsing only by wildlife, primarily mule deer, either failed to successfully regenerate, defined as producing new stems greater than 2 m tall, or regenerated at stem densities significantly lower than that on total exclusion plots. While on combined wildlife-livestock use plots, most aspen failed to successfully regenerate, or did so at even lower stem densities. Moreover, aspen successfully regenerated on livestock exclusion and combined use plots only when deer numbers were low. Similarly, ungulate herbivory had significant effects on understory species composition. In general, utilization by deer tended to eliminate shrubs and tall palatable forbs while favoring the growth of native grasses. Livestock grazing, however, tended to eliminate native grasses while promoting non-native species and bare soil. Thus, communities dominated by old-age or single-age trees are an artifact of ungulate browsing, not a biological attribute of aspen, as has been commonly assumed. There was no indication that climatic variation had any measurable effect on these aspen

communities. Instead, all the observed differences were attributable to various histories of ungulate herbivory.

INTRODUCTION

Aspen (Populus tremuloides) is an excellent indicator of forest health and ecological integrity in the southern Rockies because the species does not commonly grow from seed due to its demanding seed bed requirements (Kay and White 1995; Kay 1997a, 1997b, 1997c; White et al. 1997). In fact, there are no known instances of aspen clones having established from seed anywhere in the Intermountain West during the period of recorded history (Kay 1993). It is thought that environmental conditions have not been conducive to seedling growth and clonal establishment since shortly after the glaciers retreated 10,000 or more years ago (McDonough 1979, 1985; Jelinski and Cheliak 1992; Mitton and Grant 1996). This means that the aspen clones found throughout Utah today have likely maintained their presence on those sites for thousands of years via vegetation regeneration. Some clones in the southern Rockies are thought "to be as much as a million years old" (Cartwright and Burns 1994:2). Thus, in a sense, western aspen represents old-growth ancient forests (Peterson et al. 1995), not seral plant communities. Aspen, in fact, may be among the longest-lived organisms on Earth (Mitton and Grant 1996).

Western aspen clones are also generally quite large. In Yellowstone, for example, randomly selected aspen stands averaged more than 0.4 ha., and larger clones are common (Kay 1990). One clone in southern Utah, named Pando, contains an estimated 47,000 stems, covers 43 ha., and weighs approximately 545,500 kg, making it the largest known living organism (Grant et al. 1992, Grant 1993, McLean 1993).

Aspen seedlings are more common in the northern Canadian Rockies (Peterson and Peterson 1992) and there may be "windows of opportunity" that allow seedling establishment at infrequent, 200 to 400 year or longer, intervals (Jelinski and Cheliak 1992:728), but successful sexual reproduction of aspen is still exceedingly rare (Mitton and Grant 1996). Aspen invariably occur as clones in which all the individual trees (ramets) are genetically identical, having grown from a common root system by vegetative shoots. If aspen are lost due to advancing forest succession or overbrowsing (see below), there are no known means of reestablishing those clones (Kay 1997a, 1997b, 1997c).

In addition, aspen communities support an array of other species and have extremely high biological diversity (DeByle and Winokur 1985; Peterson and Peterson 1992, 1995). In fact, aspen has the highest biodiversity of any upland forest type in the Rockies. Bird communities, for instance, vary with size, age, and location of aspen clones, as well as with grazing intensity and history (Daily et al. 1993, Johns 1993, Westworth and Telfer 1993). So if aspen is lost, many birds and small mammals will decline; some precipitously (Ehrlich and Daily 1993).

As a relative short-lived tree (< 150 years), long-lived aspen clones are often dependent on periodic disturbance such as fire to stimulate vegetative regeneration via root suckering, and to reduce conifer competition (Bartos and Mueggler 1979, 1981; Bartos et al. 1991, 1994; Shepperd 1993; Shepperd and Smith 1993). In the absence of fire, many aspen clones in the Intermountain West will eventually be replaced by more shade-tolerant species, although climax aspen is also common (Mueggler 1988). Aspen, however, will burn only when it is leafless and when the understory plants are

dry enough to carry a fire, conditions that occur in the West only early in the spring before understory regrowth, and late in the autumn after leaf-fall and the understory plants have cured (Fechner and Barrows 1976, Brown and Simmerman 1986, DeByle et al. 1987). During both those periods, though, there are few lightning strikes and virtually no lightning-started fires in the Rockies (Kay 1990, 1995, 1996, 1997a). This would suggest that in pre-Columbian times, native burning may have been more important than lightning-started fires in maintaining aspen and other forest communities (Kay 1995, 1996, 1997a, 1997b, 1997c).

Moreover, aspen provides highly palatable forage for elk (Cervus elaphus), mule deer (Odocoileus hemionous), and livestock throughout the West (Wallmo and Regelin 1981, Nelson and Leege 1982). Aspen, however, is sensitive to repeated browsing and range use levels. High density elk populations commonly strip bark from mature aspen and severely browse aspen suckers that can prevent stand regeneration and which may eventually lead to the loss of aspen clones (Krebill 1972; Olmstead 1977, 1979; Weinstein 1979; Kay 1985, 1990; Shepperd and Fairweather 1994; Baker et al. 1997; White et al. 1997). Large numbers of mule deer can also prevent aspen regeneration (Olmstead 1979), and if not properly managed, livestock can have similar negative impacts on aspen communities (Baker 1918, 1925; Sampson 1919; Coles 1965; Weatherill and Keith 1969). Unlike herbaceous plants, the long-term grazing and fire histories of aspen communities can be judged from historical and repeat photographs (Kay and Wagner 1994).

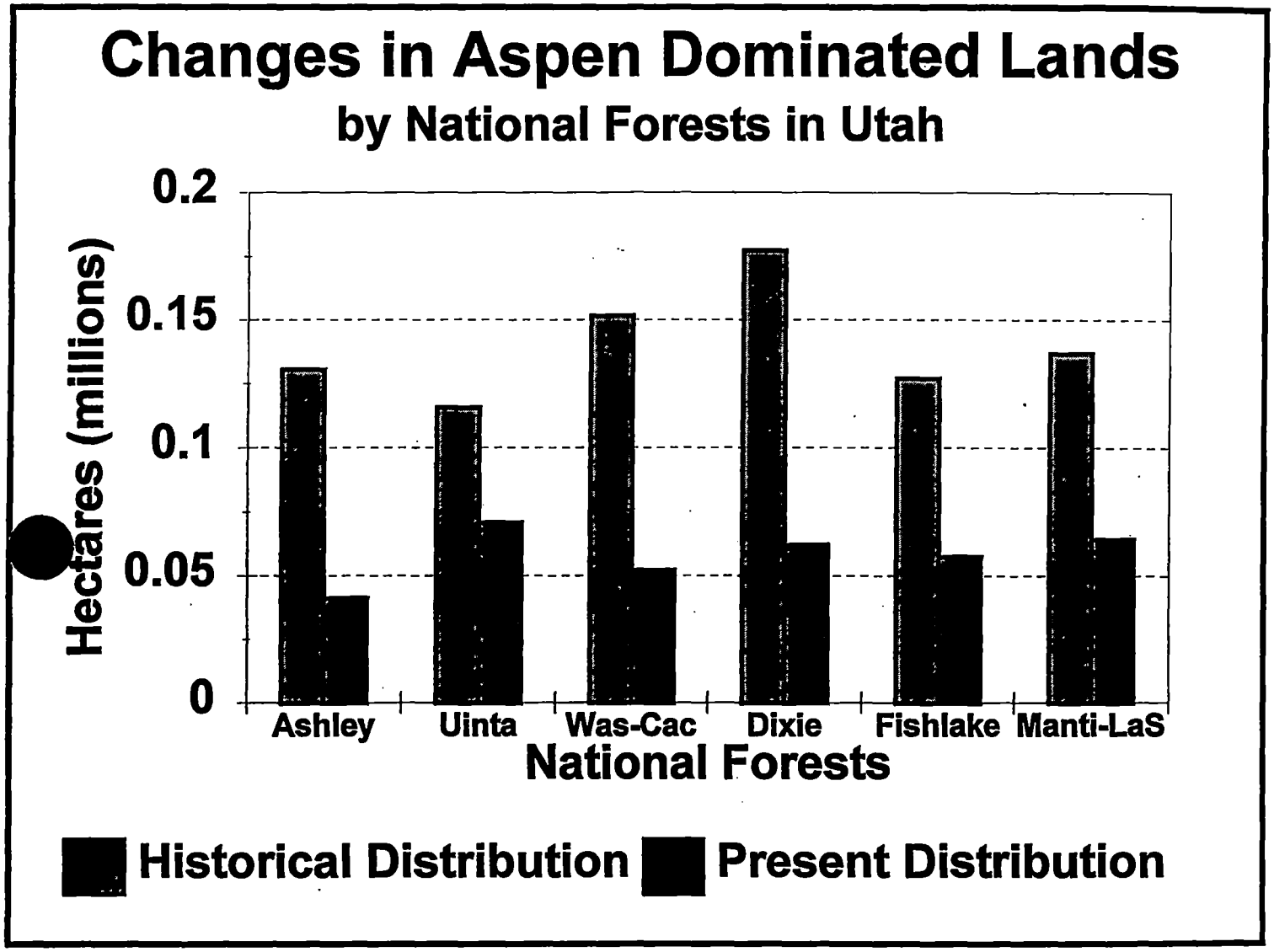
Aspen, however, has been declining throughout the Intermountain West since shortly after European settlement (Schier 1975; Schier and Campbell 1980; Kay 1997a,

1997b). Since 1962, the acreage of aspen dominated forests in Arizona and New Mexico has decreased by nearly 50% (U.S. Forest Service 1993, Cartwright and Burns 1994, Johnson 1994). While in the northern Rockies, aspen has declined by up to 90% since the late 1800s (Kay 1990, 1997a, 1997c; Kay and Wagner 1994, 1996; Kay and White 1995). On Idaho's Targhee National Forest, inventory data show that 36% of the West Camas Creek drainage was dominated by aspen in 1914, but today, aspen occupies only 4% of the area - - figures that are confirmed by repeat-photographs (Kay 1997a). In Utah, aspen has also declined from its historical distribution (Bartos and Campbell 1996). On the Dixie National Forest, for instance, there were historically over 240,000 ha of aspen while today there is only approximately 80,000 ha. Similarly, the Fishlake National Forest once contained over 200,000 ha of aspen while, today, that figure is down to 100,000 ha (see Figure 1). Furthermore, many aspen stands contain old-age or single-age trees and have not successfully regenerated for 80 years or longer (Mueggler 1989a, 1989b).

At least four hypotheses have been advanced to explain the decline of aspen in south-central Utah and throughout the Intermountain West. (1) Climatic change - - the climate was more favorable for aspen in the past and today's drier climate precludes aspen regeneration (Despain et al. 1986, Romme et al. 1995, Baker et al. 1997). (2) Fire suppression - - aspen is a seral species that will not successfully regenerate unless the overstory aspen and invading conifers are killed by fire (Houston 1973a, 1982; Loope and Gruell 1973; Gruell and Loope 1974; Despain et al 1986), and thus, modern fire suppression has adversely effected aspen. (3) Livestock grazing is preventing the growth of aspen suckers into trees (Sampson 1919, Baker 1925). And (4) repeated

Figure 1. The decline of aspen on National Forests in Utah. Historically there was more than 800,000 ha of aspen in Utah, but today there is less than 350,000 ha - - a 60% reduction. Unpublished forest inventory data, Rocky Mountain Research Station, USDA Forest Service, used with permission.

Figure 1


Changes in Aspen Dominated Lands
by National Forests in Utah
Hectares (millions)
0.2
0.15
0.1
0.05
0
Ashley
Uinta
Was-Cac
Dixie
Fishlake
Manti-LaS
National Forests
Historical Distribution
Present Distribution

browsing by mule deer and/or elk is preventing aspen sucker height growth and the successful regeneration of aspen stands (Coles 1965; Bartos and Mueggler 1979, 1981).

To test these hypotheses, I measured all the long-term, aspen-containing exclosures on the Fishlake and Dixie National Forests in south-central Utah. These exclosures were originally built to study the effect of livestock and/or wildlife use on aspen communities (Young 1956, Laycock 1969), but because the general climate is the same inside and outside the fenced plots, they can also be used to test the climatic change hypothesis (Laycock 1975). This was part of a larger project to assess the condition and trend of aspen in southern Utah. That study included repeat photopoints to evaluate long-term vegetation changes (Kay 1997a), burning and cutting aspen stands of different aspen and conifer stem densities, as well as fencing plots to exclude livestock and wildlife on treated and untreated sites to quantify interactive effects. Here, though, I only report the results from exclosures that were established during the 1930s, 1950s, 1960s, or 1970s.

METHODS

Laycock's (1969) list of range reference sites in Utah was first checked for aspen-containing exclosures on the Fishlake and Dixie National Forests. I then contacted the Forest Service employees in charge of the range programs on every district on both National Forests to determine if the exclosures listed by Laycock (1966) still existed or if there were other aspen-containing exclosures, either ones not originally mentioned by Laycock (1969), or ones built after his work had been published. This produced a list of possible study sites that were subsequently field-checked to establish whether or not the exclosures were still functional. I also searched agency files for any information that existed on the exclosures. Care will be taken to locate all previous vegetation data, any written description of permanent vegetation sampling schemes, and any old photographs.

Some of the exclosures were of a two-part design where an inside area was fenced to exclude livestock, primarily cattle, but which allowed access by deer and elk, while adjacent, unfenced outside plots were grazed by both wild and domestic ungulates. Other exclosures were of a three-part design where one area was fenced to exclude all ungulates, one area was fenced to exclude only livestock, and a third area was open to wild and domestic ungulates. This permitted the effects of wildlife to be measured separately from those of livestock.

At each exclosure, I first resampled any permanent aspen plots previously established by the Forest Service or other agencies, and I rephotographed all permanent photopoints. Next, I placed 2 or more 2 x 30 m belt transects in

representative aspen communities within each of the various parts of each exclosure (Kay 1990, 1997c). To facilitate data recording, I subdivided each 30 m transect into 3 m segments and then recorded the number of live aspen stems by size classes within each 3 m segment. I used the following size classes: (1) stems less than 2 m tall, (2) stems greater than 2 m tall but less than 5 cm diameter at breast height (DBH), (3) stems between 6 and 10 cm DBH, (4) stems between 11 and 20 cm DBH, and (5) stems greater than 21 cm DBH. Ages of aspen within each size class were determined by counting annual rings. The ages of large aspen were obtained with the aid of an increment borer while smaller stems, usually those less than 5 cm DBH were cross sectioned. Stems less than 2 m tall were not aged (Kay 1990, 1997c).

Within each aspen stand, I also recorded the following information (Kay 1990, 1997c): (1) elevation as determined from topographic maps; (2) Universal Transverse Mercator (UTM) grid coordinates, again estimated from topographic maps; (3) aspect - - north, northeast, east, southeast, south, southwest, west, and northwest; (4) estimated slope in percent; (5) estimated stand size in meters; (6) bark damage - - percent of stems that exhibited old black-scar, ungulate bark damage and the percent of stems with new or recent bark damage - - wounds that had not yet healed over with black-colored bark, usually less than two years old (Krebill 1972); (7) an estimate of the mean percent of each stem that had been damaged by ungulate bark stripping; (8) if the stand had newly regenerated stems greater than 2 m tall but less than 5 cm DBH, an estimate of the percent that showed evidence of ungulate highlining - - where the ungulates browse off all the lower branches as high as the animals can reach, usually 2-3 m; and (9) the percent of stems less than 2 m tall that exhibited ungulate browsing. Items 6 to

9 provided an estimation of past ungulate use (Kay 1997c). Only elk or moose (Alces alces) strip-off and eat the bark of aspen, and bark damage usually occurs during winter when other foods are in short supply. Mule deer do not strip aspen bark, but mule deer, elk, and moose all browse aspen when the plants are available. As explained more fully below, mule deer have been the primary wild herbivore in south-central Utah since at least the 1930s, while moose were only recently transplanted into the area, and elk populations were very low until the 1980s.

In addition, at each exclosure complex I recorded the number and species of conifers on the 2x30 m belt transects that were used to count aspen stems (Kay 1990, 1997c). Conifers were recorded by the same five size classes that were used for aspen. While a 2x30 m belt transect is adequate to measure aspen stem dynamics and conifer seedlings (Bartos and Mueggler 1979, 1981; Kay 1990; Bartos et al. 1994), that sized plot tends to underestimate the more widely spaced conifers. To overcome this problem, I estimated the total percent conifer canopy cover in each aspen stand according to guidelines established by Mueggler (1988).

Finally, at 1 m intervals to the right of each of the belt transects centerline, $0.1m^2$ (0.2mx0.5m) plots were used to estimate canopy-cover of understory plants, bare soil, and rock (Daubenmire 1959). Within each treatment - - total exclusion and/or livestock exclusion or combined use - - readings from all the $0.1m^2$ understory plots were averaged to produce a mean and other statistical parameters. Similarly, within each treatment, aspen and conifer stem densities on each of the 2x30m belt transects were used to produce statistical parameters. The means of the various treatments within

each exclosure complex were then compared using Student's t tests (Sokal and Rohlf 1981).

RESULTS

Many of the aspen-containing exclosures listed by Laycock (1969) for south-central Utah no longer exist. Some have not been maintained and are no longer functional, while others have been removed by the U.S. Forest Service. Thus, I was able to locate and measure only nine aspen exclosures (Table 1) - - five on the Dixie National Forest (Pot Holes, Park Pasture, Blind Lake, Riddle Swale, and Woodchuck), three on the Fishlake National Forest (Grindstone Flat, Big Flat, and Hancock), and one on Utah State Trust Lands (Parker Mountain).

Of the exclosures listed by Laycock (1969:7-11) on the Dixie - - Six Lakes, Tippetts Valley, Webster Flat, and Cougar Hollow no longer exist. Three exclosures listed by Laycock as not containing aspen were actually found to contain that species. Riddle Swale and Pot Holes contain abundant aspen and were measured, but Blowup contains only a few stems and was not measured. Laycock did not mention the Park Pasture exclosure on the Teasdale Ranger district, but it too contains abundant aspen and was sampled during this study.

Of the aspen exclosures listed by Laycock (1969:11-14) for the Fishlake - - Merchant Valley, Timid Springs, Misery Creek, Rockwood, West Corn Creek, and Washburn Reservoir are no longer functional research sites. Laycock also did not mention the two aspen exclosures at Big Flat. The larger of the two and the one measured by Mueggler and Bartos (1977) has been removed, but the smaller fenced plots remain and were measured during 1996.

Only one aspen-containing exclosure has been built in south-central Utah since Laycock (1969) completed his study. A five-part (see below) exclosure was constructed

Table 1. Location and description of aspen containing exclosures in south-central Utah.

Exclosure	Land ownership*	Location T	R	S	Date established	Size (m) Livestock exclusion	Total exclusion	Elevation (m)	Main aspect	Vegetation type**
Pot Holes	DNF	30S	3E	27	1958	62x63	None	2743	NW	A,S/G
Park Pasture	DNF	31S	5E	22	1957	88x94	None	2652	NE	A,G
Blind Lake	DNF	30S	4E	24	1958	44x117	None	2984	SE	A,G
Riddle Swale	DNF	33S	1W	19	1957	65x76	65x113	2554	N	A,S/G,C
Woodchuck	DNF	31S	2 1/2W	33	1947	63x63	63x63	2804	S	A,S/G
Grindstone Flat	FNF	29S	4W	29	1934	46x63	46x63	2816	S	A,C
Big Flat	FNF	29S	4W	18	1934	8x9	8x9	3158	S	A
Hancock	FNF	26S	1E	11	1962	61x61	61x61	3054	SE	A,C
Parker Mountain (a.k.a. Pine Peaks)	UT	28S	1W	26	1974	100x100	100x100	2804	E	A,S/G

* DNF = Dixie National Forest, FNF = Fishlake National Forest, UT = Utah State School Trust Lands.
** Vegetation types within the exclosurs. A = aspen, S/G = sagebrush/grasslands, G = grasslands, and C = conifers.

by the Bureau of Land Management (BLM) in 1974 on Parker Mountain, which lies between the Dixie and Fishlake National Forests. Subsequently, that site, as well as other lands on Parker Mountain, were transferred to the State of Utah in exchange for state lands within various Utah national parks.

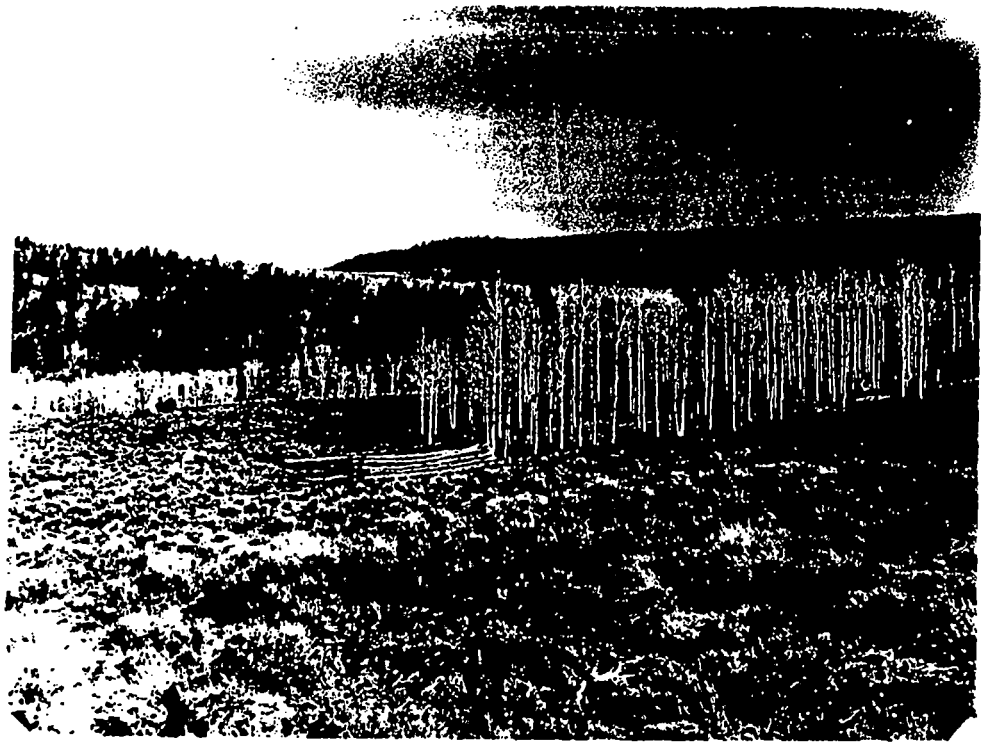
Unfortunately, except for Grindstone Flat, I was not able to locate any previously collected data on aspen communities inside or outside any of the aspen-containing exclosures that still exist in south-central Utah. In some cases, the U.S. Forest Service could not even locate the original files for the exclosures, while at others, the agency had collected data on only grassland communities, but not aspen - - the latter was also true at the exclosure on Parker Mountain. At only four exclosures (Pot Holes, Park Pasture, Grindstone Flat, and Parker Mountain) was I able to locate photographs in which the original enclosed aspen community was clearly visible.

Pot Holes

Laycock (1969:11) listed a 1 acre Pot Holes exclosure on the west side of Boulder Mountain that was supposedly erected in 1929, but that is not correct. As shown in Figure 2, a small pole exclosure was constructed in a sagebrush (Artemisia spp.) community during 1929 adjacent to an aspen stand. Then in 1958, the original exclosure, as well as part of adjoining aspen community was enclosed in a 62x62 m fenced plot that excludes livestock, but not deer or elk (Table 1). Shortly thereafter, the old pole exclosure was removed.

Figure 2. Repeat photoset of the Pot Holes exclosure. (a) This photo was taken in October 1958 shortly after the new 1 acre exclosure had been constructed. Note the wooden pole exclosure erected in 1929 and the new wire fence on the hillside behind the old fenced plot. The photopoint is just inside the southwest corner of the new exclosure and is viewed to the northeast. Shown in the distance are the more heavily timbered slopes of Boulder Mountain. U.S. Forest Service photo. (b) That same site in August 1995. With projection from livestock grazing, the aspen stand regenerated and spread inside the exclosure, including the site once occupied by the old wooden exclosure. This occurred during the early 1970s when mule deer numbers were low (see below), but as deer numbers increased, those animals then high-lined the regenerated aspen and prevented new suckers from growing more than 1 m tall. There also appears to have been an increase in grass cover inside the exclosure, while rabbitbrush and sagebrush appear to have declined.

Figure 2



With protection from cattle grazing, the aspen stand successfully regenerated without fire or other disturbance, and increased in size inside the exclosure (Figure 1). This occurred during the early 1970s when mule deer numbers were low (see below), but as deer numbers increased in subsequent years, those animals consumed all the lower branches from the newly grown aspen, termed high-lining, and also prevented new suckers from growing more than 1 m tall. The aspen stand inside the exclosure is now composed of multi-sized, multi-aged stems, while there has been little regeneration outside the exclosure (Table 2). Since the exclosure fence bisects a single aspen clone, this cannot be due to genetic or climatic differences. Aspen stem numbers and understory canopy cover were measured on three 2x30 m belt transects inside the exclosure with a similar number of plots established outside.

This site is at the lower limit of tree growth on the west side of Boulder Mountain, and as such, there are few conifers in the aspen stand. As shown in Figure 2, the exclosure straddles the aspen sagebrush-grassland ecotone. The largest live aspen were 28 cm DBH and 85± years old. While the 6-7 cm DBH stems were 20-21 years old and the 4 cm stems were 10-12 years of age. There was fresh deer sign within the exclosure when it was measured during August 1995. At this elevation, the conifers are mostly ponderosa pine (Pinus ponderosa) and a few Douglas fir (Pseudotsuga menziesii).

There were also major differences in understory species composition inside and outside this exclosure (Table 3). Unpalatable shrubs, such as rabbitbrush (Chrysothamnus spp.) had greater frequency and canopy cover outside the exclosure,

Table 2. Mean aspen stem densities by size classes and estimated conifer canopy cover inside and outside exclosures in south-central Utah.

Exclosure	Mean aspen stem density by size classes (stems/ha)*					Conifer canopy cover
	2m	2m-5cm	6-10cm	11-20cm	>20cm	
Pot Holes						
Livestock exclusion**	7,348	3,791	2,221	618	333	<1%
Outside	9,018	668	0	55	55	<1%
Park Pasture						
Livestock exclusion	1,221	4,676	3,758	1,378	250	<1%
Outside	459	835	835	0	584	<1%
Blind Lake						
Livesock exclusion	9,574	8,684	3,228	1,057	556	<1%
Outside	8,963	6,568	167	55	668	<1%
Riddle Swale						
Total exclusion	7,228	4,670	2,780	1,890	168	<1%
Livestock exclusion	8,613	2,446	834	0	449	<1%
Outside	1,890	0	111	0	222	5%
Woodchuck						
Total exclusion	5,177	4,787	2,394	1,169	390	None
Livestock exclusion	946	0	56	779	390	None
Outside	2,088	0	0	1,086	0	None
Grindstone Flat***						
Total exclusion	NA	2,505	3,396	1,614	333	30%
Livestock exclusion	NA	0	222	835	668	40%
Outside	NA	0	0	167	752	25%
Hancock						
Total exclusion	5,288	7,738	1,225	557	445	30%
Livestock exclusion	2,728	0	0	0	557	50%
Outside	4,676	0	0	0	500	60%
Parker Mountain						
Total exclusion	974	2,672	1,308	84	500	None
Livestock exclusion	4,509	389	0	0	84	None
Outside	1,030	28	0	0	306	None
Total						
Total Exclusion	4,667	4,474 [a]	2,221 [a]	1,063 [a]	367	-
Livestock Exclusion	4,990	2,498	1,290	820	411	-
Outside	4,018	1,318 [a]	139 [a]	170 [a]	386	-

* Aspen stem size classes: 2m = stems less than 2m tall; 2m-5cm = stems greater than 2m tall but 5 cm or less diameter at breast height (DBH); 6-10 cm = stems 6-10cm DBH; 11-20cm = stems 11-20cm DBH; and >20cm = stems greater than 20cm DBH.

** Livestock exclusion = fenced to exclude either cattle or domestic sheep; total exclusion = fenced to exclude all ungulates, domestic and wild; and outside = unfenced area grazed by all classes of ungulates.

*** Includes only uncut stands - - see text.

NA Stems less than 2m tall were not counted because most had been consumed by a recent fire - - see text.

Table 3. Understory species composition inside and outside the Pot Holes exclosure.

	Mean percent canopy cover and frequency by treatment			
	Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs				
Artemisia tripartata	3	0.4	9	2.2
Artemisia tridentata	-	0.0	3	0.6
Chrysothamnus nauseosus	1	0.1	11	3.7
Chrysothamnus viscidiflorus	21	7.9	40	16.1
Grasses				
Stipa comata	90	36.2	66	11.1
Muhlenbergia wrightii	2	0.2	14	1.7
Sitanion hystrix	46	8.2	58	8.7
Festuca idahoensis	46	11.3	90	15.9
Forbs				
Lupinus caudatus	8	2.6	22	5.7
Castilleja linariafolia	11	2.8	2	0.2
Antennaria microphylla	-	0.0	54	11.9
Rock	1	0.2	-	0.0
Bare soil	1	0.1	45	8.7
Litter	88	30.7	64	13.0
Total grass	-	55.9	-	37.4

while needle-and-thread grass (Stipa comata) was more abundant inside the fenced plot, as was total grass canopy cover. Indian paintbrush (Castillega linariafolia) was more abundant where livestock had been excluded, while the unpalatable forb Antennaria microphylla was more prevalent outside the exclosure. There was also more bare soil and less litter outside the exclosure. All differences were significant at $p<.05$, Student's t test.

Park Pasture

When the Park Pasture exclosure was erected in 1957 on the east side of Boulder Mountain that area was a heavily used joint sheep-cattle allotment, but domestic sheep were eliminated in 1963 and cattle herbivory subsequently reduced through implementation of a deferred rotational grazing system (U.S. Forest Service 1995). Historically, the area was also grazed by a large mule deer population, but that herd has since declined (see below). When the exclosure was built, elk were rare but that species is now common. In fact, several fresh elk beds were observed inside the exclosure when this site was visited during August 1995. Four 2x30 m transects were measured inside the exclosure with a similar number recorded outside.

As shown in Figure 3, there were no young aspen in 1957, but with exclusion of livestock, aspen regenerated and spread inside the exclosure. This exclosure is also situated on an aspen-grassland ecotone and there are few conifers in the clone - - ponderosa pine, Douglas fir, spruce (Picea sp.), and subalpine fir (Abies lasiocarpa) being the most common species in the immediate area. The largest aspen were 38-

Figure 3. Repeat photoset of the Park Pasture exclosure. (a) This photo was taken in September 1958 shortly after the exclosure was constructed and shows no aspen regeneration. The area had been heavily grazed - - note the sheep near the stream and the eroding gully in the lower right of the photo. The photopoint is located outside the southeast corner of the exclosure and is viewed northwest to Boulder Top. U.S. Forest Service photo. (b) That same site in August 1995. The aspen clone has regenerated and spread inside the exclosure, while the gully has revegetated both inside and outside the exclosure. Cattle had not yet grazed this pasture when this photograph was taken. Note how deer and elk have high-lined the regenerated aspen inside the exclosure and prevented recent aspen suckers from increasing in height. Photo by Charles Kay (No. 3910-20).

Figure 3

40 cm DBH and were 105-115 years old. Inside, but not outside the exclosure, there were numerous 10-15 cm DBH stems that were 25-30 years of age (Table 2). These began growth during the mid-1960's when combined high deer populations and cattle grazing apparently prevented aspen regeneration outside the exclosure. When deer numbers fell during the early to mid-1970s (see below), however, aspen regenerated both inside and outside the exclosure, but at significantly higher stem densities where cattle also were excluded (Table 2). The 7-9 cm DBH stems were all approximately 20 years old while the 5 cm DBH stems were 14-15 years of age. As deer numbers rebounded during the 1980s, those animals both highlined the regenerated aspen and prevented new suckers from increasing in height growth. There was, however, little difference in understory species composition or frequency (Table 4).

Blind Lake

The Blind Lake exclosure was built in 1958 on the north side of Boulder Mountain in an area comprised primarily of aspen and small meadows. There are few conifers, primarily spruce, in the exclosure or in the surrounding area (Table 1). Aspen stems inside the exclosure are multi-sized and multi-age, and began regenerating shortly after the exclosure was erected (Table 2). That is to say, the elimination of cattle grazing reduced herbivory on aspen suckers and allowed those stems to grow into the larger size classes. Aspen outside the exclosure regenerated approximately 20 years ago when deer numbers plummeted (see below) despite continued grazing by cattle. The largest aspen were 30-38 cm DBH and 95-105 years old, while the 4-5 cm DBH stems

Table Understory species composition inside and outside ark Pasture exclosure.

	Mean percent canopy cove and frequency by treatment			
	Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs				
Potentilla fruticosa	4	0.3	5	0.7
Symphoricarpos oreophilus	10	4.8	2	0.3
Grasses				
Poa pratensis	55	37.7	40	21.0
Festuca thurberi	15	6.1	28	11.2
Bromus ciliatus	2	0.2	3	0.8
Stipa comata	27	7.7	29	6.8
Sitanion hystrix	6	1.0	12	1.8
Myhlenbergia wrightii	-	0.0	18	5.0
Forbs				
Traxacum officinale	-	0.0	14	2.2
Vicia americana	83	25.2	72	26.5
Rock	2	1.0	2	0.7
Bare soil	-	0.0	-	0.0
Litter	37	15.7	61	22.2
Total grass	-	52.7	-	46.6

were 18-25 years of age. Three belt transects inside and three outside were used to record aspen stem densities and understory species composition. Based on the distribution of new stems, aspen inside the exclosure has spread, replacing a largely grassland community.

Outside the exclosure there was significantly less snowberry (Symphoricarpos oreophilus) ($p<.01$) and Ligusticum porteri ($p<.001$), a tall palatable forb, while there was significantly more bare soil ($p<.001$) and dandelion (Traxacum officinale) (Table 5). In general, there were more palatable forbs inside the exclosure, while unpalatable forbs were more common outside (Table 5). There was also significantly more ($p<.001$) vegetative cover inside the exclosure than out, at least in the aspen understory.

Riddle Swale

Unlike the three previous exclosures, Riddle Swale is a three-part exclosure with a total exclusion portion, a livestock exclusion portion, and an outside plot open to both wildlife and cattle (Table 1). Aspen stem densities and understory species composition were recorded on three 2x30 m belt transects in each of the three parts of this exclosure. The site is located on the west side of Escalante Mountain at the ecotone between aspen, sagebrush, and pinyon-juniper. Utah juniper (Juniperus osteosperma) and pinyon pine (Pinus monophylla) are found both inside and outside the exclosure, as are a few ponderosa pine and Douglas fir.

Aspen inside the total exclusion part began regenerating shortly after the exclosure was constructed in 1957 and the stems are now multi-sized and multi-aged

Table 5. Understory species composition inside and outside the Blind Lake exclosure.

Species	Mean percent canopy cover and frequency by treatment			
	Livestock exclusion		Outside	
	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs				
Rosa woodsii	11	3.2	11	2.9
Ribes sp.	8	2.9	4	1.4
Symphoricarpos oreophilus	58	29.1	40	11.8
Juniperus communis	-	0.0	1	0.4
Grasses				
Poa pratensis	-	0.0	28	2.8
Bromus ciliatus	18	1.7	18	1.7
Festura thurberi	14	3.4	11	1.3
Stipa comata	3	1.0	-	0.0
Forbs				
Ligusticum porteri	38	15.9	-	0.0
Lupinus argenteus	34	15.8	24	5.6
Potentilla gracilis	2	1.3	-	0.0
Traxacum officinale	43	7.9	79	28.3
Achillea millefolium	1	0.1	17	1.3
Fragaria virginiana	16	1.2	3	0.2
Rock	18	6.5	19	9.0
Bare soil	-	0.0	43	11.6
Litter	37	10.0	53	21.3
Rock, bare soil, litter	-	16.5	-	41.9
Total vegetation	-	83.5	-	48.1
Total forbs	-	42.2	-	35.4
Total grasses	-	6.1	-	5.8

(Table 2 - - also see Kay 1997a:8). Based on the distribution of new stems, aspen inside the total exclusion part has also spread, replacing sagebrush-grasslands. While in the livestock exclusion part of the exclosure, aspen only regenerated when deer numbers experienced a sharp decline around 20 years ago (see below). Where both cattle and deer have grazed, however, few aspen stems have ever been able to attain more than 2 m in height (Table 2 - - also see Kay 1997a:8). As the deer population recovered, however, those animals high-lined all the previous aspen regeneration inside the livestock exclusion part of the exclosure and have prevented any new aspen suckers from growing more than 1 m tall. The largest aspen at this site were 23-26 cm DBH and 72-78 years old, while the 8-10 cm DBH stems were 20-25 years of age. The 3-5 cm stems were 14-20 years old.

There were also major differences in understory species composition (Table 6). Deer use and combined use eliminated Indian paintbrush, while cattle use significantly ($p<.01$) reduced the canopy cover of native grasses. Conversely, sagebrush increased under deer use, and even more so under combined use. Bare soil and rock were not recorded where ungulate herbivory was absent, but increased to 6.4% canopy cover where only wildlife grazed and to 27.2% under combined deer-cattle use ($p<.01$).

Woodchuck

Woodchuck is a three-part exclosure that was built on the northeast slope of Mount Dutton in 1947 (Table 1). Although this exclosure is at over 2,800 m, it is

Table 6. Understory species composition inside and outside the Riddle Swale exclosure.

	Mean percent canopy cover and frequency by treatment					
	Total exclusion		Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs						
Artemisia tripartata	3	0.4	-	0.0	21	6.8
Artemisia tridentata	20	5.2	26	9.3	24	7.7
Symphoricarpos oreophilus	7	1.8	18	6.3	7	0.9
Purshia tridentata	-	0.0	-	0.0	2	1.9
Juniperus osteosperma	7	3.3	-	0.0	8	5.9
Chrysothamnus nauseosus	1	0.1	6	2.0	4	0.4
Rosa woodsii	2	0.7	-	0.0	-	0.0
Grasses						
Sitania hystrix	8	0.6	16	1.7	-	0.0
Elymus trachycaulus	39	3.8	27	3.0	11	0.8
Stipa comata	77	22.2	78	14.7	54	3.6
Bromus ciliatus	21	2.3	33	3.7	-	0.0
Forbs						
Galium sp.	38	3.9	28	3.6	-	0.0
Castilleja linariafolia	54	6.6	-	0.0	2	0.2
Rock	-	0.0	-	0.0	28	8.5
Bare soil	-	0.0	11	6.4	50	18.7
Litter	90	48.5	88	48.9	72	41.6
Bare soil and rock	-	0.0	-	6.4	-	27.2
Total grass	-	28.9	-	23.1	-	4.4
Total *Artemisia* sp.	-	5.6	-	9.3	-	14.5

situated at the lower boundary for aspen in this area and the exclosure is surrounded by extensive sagebrush-grasslands. No conifers are present. Cattle have historically used this allotment and deer numbers have also been high. In fact, every time I have visited this exclosure complex, I have flushed deer out of the livestock exclusion part. Elk have only recently become common on Mount Dutton (see below) and do not appear to heavily use this isolated patch of aspen, probably because it is too far from other cover (Lyon et al. 1985, Brunt 1990:88). Three 2x30 m belt transects were placed in each of total and livestock exclusion parts, while only two belt transects were placed in the outside aspen due to the latter's more limited area.

Aspen within the total exclusion part is multi-sized and multi-aged, began regenerating shortly after the exclosure was constructed (Table 2), and based on the distribution of new stems, has spread, replacing sagebrush-grassland. While no new aspen stems have ever attained heights of 2 m or more in either the livestock exclusion part or the combined use area (Table 2). Thus at this site, the deer population has not decreased enough since 1947 to allow aspen to regenerate even where cattle have been excluded. The largest aspen were 25-30 cm DBH and 100± years old while aspen in the 15-16 cm size class were 65-70 years of age. Apparently, something occurred during the late 1920s and early 1930s that allowed some aspen in this stand to successfully regenerate before it was enclosed.

Deer use also significantly reduced wild rose (Rosa woodsii), snowberry, lupine (Lupinus caudatus), and Indian paintbrush, but favored the growth of native grasses, especially needle and thread (all $p<.01$) (Table 7). While cattle grazing significantly reduced native grass cover ($p<.001$) and significantly increased bare soil ($p<.01$). Non-

Table 7. Understory species composition inside and outside the woodchuck exclosure.

	Mean percent canopy cover and frequency by treatment					
	Total exclusion		Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs						
Rosa woodsii	3	1.6	-	0.0	-	0.0
Symphoricaipos oreophilus	42	20.4	10	1.6	3	0.5
Chrysothamnus viscidiflorus	-	0.0	8	1.6	-	0.0
Artemisia tridentata	6	2.4	11	3.7	17	6.2
Grasses						
Stipa comata	28	9.9	57	22.2	18	1.8
Stipa lettermanii	14	2.3	11	2.2	-	0.0
Elymus trachycaulus	42	8.0	21	4.3	5	0.7
Bromus ciliatus	31	4.9	13	1.8	1	0.2
Festuca idahoensis	1	0.1	19	4.3	-	0.0
Sitania hystrix	8	0.9	7	1.1	-	0.0
Poa pratensis	2	1.9	32	23.7	95	50.9
Sedges						
Carex sp.	2	0.2	17	4.2	-	0.0
Forbs						
Lupinus caudatus	82	40.4	3	0.3	14	3.1
Castilleja linariafolia	20	2.8	-	0.0	-	0.0
Rock	-	0.0	6	1.0	-	0.0
Bare soil	-	0.0	1	0.6	28	10.5
Litter	16	4.1	64	20.7	83	25.8
Total native grasses	-	26.1	-	35.9	-	2.7
Total introduced grasses	-	1.9	-	23.7	-	50.9
Total vegetation	-	95.9	-	77.7	-	63.7

native Kentucky bluegrass (Poa pratensis) increased from 1.9% canopy cover in the total exclusion exclosure, to 23.7% under deer only use ($p<.001$), and to 50.9% with the addition of cattle grazing ($p<.01$). Total vegetative understory cover also declined significantly ($p<.01$) from 95.9% in the non-grazed area to 77.7% in the wildlife only area to 63.7% in the combined use area.

Grindstone Flat

The three-part exclosure at Grindstone Flat (Table 1) was constructed in 1934 and was previously evaluated by the Utah Department of Fish and Game (since renamed the Utah Division of Wildlife Resources) during the 1950s (Young 1956) and remeasured by the U.S. Forest Service in 1975 (Mueggler and Bartos 1975). Part of the site was originally clear-cut and those aspen stems were used to build the pole exclosure fences (see photos in Mueggler and Bartos 1977). One-third of each exclosure, though, as well as all of the outside aspen were left uncut. Thus, this produced an uncut total-exclusion area, a cut total-exclusion area, an uncut livestock-exclusion area, a cut livestock-exclusion area, and an uncut outside area (Young 1956).

As reported by Young (1956) and Mueggler and Bartos (1977), aspen quickly regenerated inside the cut total-exclusion area, while deer use prevented aspen regrowth in the cut and uncut livestock-exclusion areas, as well as on outside plots. In addition to the photographs published by Mueggler, I located a six photo panorama at the National Archives in Washington D.C. (Record Group 95G, numbers - - left to right - - 421764, 421765, 421766, 421767, 421768, and 421769) that was taken by the U.S.

Forest Service in 1941 and which shows the above described aspen regeneration pattern. As reported by Mueggler and Bartos (1977), aspen in the uncut total-exclusion portion also successfully regenerated, while spruce and subalpine fir heavily invaded both cut and uncut areas.

Since this site had not been measured in over 20 years, it was scheduled to be included in this study, but a week before I was to visit the area, the exclosure and much of the surrounding lands were burned by the Pole Creek wildfire during late June 1996. Not only was the old wooden exclosure fence turned to ash, but much of the vegetation inside the exclosure complex was burned, as well.

The uncut total-exclusion and uncut livestock-exclusion areas were completely consumed by flames, as was the surrounding outside aspen. In contrast, the cut total-exclusion area was largely unburned while the cut livestock-exclusion area did not burn at all. This pattern is probably related to the amount of dead aspen stems on the ground and the amount of conifers that had invaded the variously treated areas. Conifer canopy cover was highest in the outside uncut aspen while it was lower in both the uncut total and uncut livestock-exclusion areas, and lower still in the total and livestock-exclusion cut areas (Table 8). Similarly, there were more downed aspen stems on the uncut areas than on the cut plots, as all the old aspen had been felled and removed in 1934. The cut livestock-exclusion area did not burn because it had been converted to a grass-forb community by mule deer herbivory and was too green to carry a fire when the area burned. The same was true of the adjacent meadow, which remained unburned despite the fact that dried cattle dung in that meadow was ignited by flying sparks and totally consumed by fire (Kay unpub. photos).

Since this is one of only two long-term aspen containing exclosures on the Fishlake National Forest, the Forest Service elected to rebuild the exclosure fences in their original configuration. Thus, I measured aspen stem densities at this site during September 1996. This was possible because the larger-sized live aspen stems were too green to have been consumed by the fire. I did not, however, recorded aspen stems less than 2 m tall, as many of those had been removed by fire. Similarly, I did not measure understory species composition.

Four 2x30 m belt transects were established in outside areas, while three belt transects were measured in each of the uncut total-exclusion, cut total-exclusion, cut livestock-exclusion, and uncut livestock-exclusion areas. Of most relevance to this study is the fact that aspen in the uncut total-exclusion area successfully regenerated and produced a multi-aged stand prior to the fire, while aspen in the uncut livestock-exclusion and outside areas produced no new stems greater than 2 m tall due to ungulate herbivory (Table 8).

Also of interest, aspen in the uncut total-exclusion area had a lower rate of conifer invasion than either the wildlife or combined grazing areas (Table 8). I was not able to core any of the unburned outside aspen stems due to extensive heart rot, but the largest trees were 38-44 cm DBH. In 1975 Mueggler and Bartos (1977:3) recorded a 41 cm DBH aspen that was 175 years old, so the few remaining, unburned, aspen trees were likely approaching 200 years, or near the maximum age recorded for aspen stems in the Intermountain West (Jones and Schier 1985).

Table 8. Aspen stem densities by size classes and estimated conifer canopy cover inside and outside the Grindstone Flat exclosure. 1975 data from Mueggler and Bartos (1977:4).

Treatment	Sample size*	Mean aspen stem density by size classes (stems/ha)**					Conifer canopy cover
		2m	2m-5cm	6-10cm	11-20cm	>20cm	
Total exclusion							
Cut	3	NA***	1,336	5,567	2,950	0	20%
Uncut	3	NA	2,505	3,396	1,614	333	30%
Livestock exclusion							
Cut	3	NA	0	0	0	0	10%
Uncut	3	NA	0	222	835	668	50%
Outside	4	NA	0	0	167	752	60%
	1975 Data						
Total exclusion							
Cut		5,198	2,228	8,564	396	0	
Uncut		2,772	2,970	3,118	1,386	99	
Livestock exclusion							
Cut		297	0	0	0	0	
Uncut		891	0	990	841	446	
Outside		7,178	0	1089	3,168	446	

* Sample size = the number of 2x30m belt transects used to count aspen stems.

** Aspen stem size classes: 2m = stems less than 2m tall; 2m-5cm = stems greater than 2m tall but 5cm or less diameter at breast height (DBH); 6-10cm = stems 6-10cm DBH; 11-20cm = stems 11-20cm DBH; and >20cm = stems greater than 20cm DBH.

*** Stems less than 2m tall were not counted because most had been consumed by the recent fire - - see text.

Big Flat

For unknown reasons, the large three-part array of aspen exclosures measured by Mueggler and Bartos (1975) at Big Flat were subsequently removed by the Forest Service, but the set of smaller three-part exclosures was not (Table 1). The larger exclosures were laid out and designed similar to the ones at Grindstone Flat - - that is, parts were cut in 1934 while others were not. The area within the smaller exclosures, as well as on the outside plot, however, had all been clear-cut, and the aspen stems removed in 1934. Thus, the data on these treated areas is not directly comparable to the uncut stands measured at the other aspen exclosures. In addition, I had to modify my sampling methods because the existing total-exclusion and livestock-exclusion exclosures would not accommodate 2x30 m transects. Instead, I counted all the aspen stems within each exclosure, as well as on a comparable sized outside plot, and I recorded understory species composition on 20 randomly placed 0.1m^2 plots in each of the three areas. Moreover, I counted all the Indian paintbrush and green gentain (Frasera speciosa) plants inside the total exclusion and livestock-exclusion exclosures, as well as on a comparable-sized outside plot. These exclosures are on a cattle allotment and mule deer have been the principle wild ungulate.

Similar to what Mueggler and Bartos (1977) reported for the larger Big Flat exclosure, aspen on the smaller total-exclusion site successfully regenerated and produced multi-sized stems, while both the livestock exclusion and outside plots did not (Table 9). There were no conifers on any of the three plots and conifers, primarily

Table 9. Aspen stem densities by size classes inside and outside the Big Flat exclosure. The stand was cut in 1934.

	Aspen stem density by size classes (stems/ha)*				
Treatment	2m	2m-5cm	6-10 cm	11-20cm	>20 cm
Total exclusion	10,817	6,341	1,865	2,984	0
Livestock exclusion	7,937	0	0	0	0
Outside	5,557	0	0	0	0

* Aspen stem size classes: 2m = stems less than 2m tall; 2m-5cm = stems greater than 2m tall but 5cm or less diameter at breast height (DBH); 6-10cm = stems 6-10cm DBH; 11-20cm = stems 11-20cm DBH; and >20cm = stems greater than 20cm DBH.

spruce and subalpine fir, were also rare in the surrounding uncut aspen. The largest uncut aspen were 38 cm DBH and 135± years old.

There were also major differences in understory species composition (Table 10). Grazing by deer effectively eliminated Indian paintbrush and green gentian, while the addition of cattle grazing significantly increased unpalatable forbs, as well as the amount of bare soil. Grazing by deer promoted the growth of native grasses, but cattle grazing had the opposite effect. Grazing also reduced the density of Indian paintbrush plants from 65,648/ha in the ungrazed area to 3,970/ha in the wildlife only grazed area to zero in the combined use area. The same was true for green gentian - - 15,666/ha in the ungrazed area with zero in both the wildlife and combined grazed areas.

Hancock

Although this three-part exclosure is listed by Laycock (1975) as being situated on Hancock Flat, it is not (Table 1). Instead, it is located above Doctor Canyon approximately 3 km southeast of Hancock Flat and 1 km northeast of Rust Spring. Nevertheless, I have retained the name Hancock to avoid confusion with earlier publications. Moreover, unlike the other exclosures in this study, Hancock is on a sheep allotment, but mule deer have still been the most abundant wild ungulate. Aspen and conifer stem densities were measured on three 2x30 m belt transects in each of the total exclusion, livestock exclusion, and outside areas, as was understory species composition. In addition, I measured the height, crown diameter, total number of flower stalks, and the number of grazed flower stalks on 25 Indian paintbrush (C. miniata)

Table 10. Understory species composition inside and outside the Big Flat exclosure.

	Mean percent canopy cover and frequency by treatment					
	Total exclusion		Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Forbs						
Castilleja linariaefolia	95	30.0	-	0.0	-	0.0
Lupinus argenteus	70	23.5	55	29.5	5	1.5
Frasera speciosa	25	5.5	-	0.0	-	0.0
Fragaria virginiana	65	7.0	30	1.5	85	7.0
Potentilla glandulosa	40	8.0	45	5.5	10	1.0
Traxacum officinale	15	1.5	15	1.2	80	6.5
Senecio sp.	10	2.0	-	0.0	-	0.0
Helenium hoopesii	-	0.0	10	1.5	60	9.0
Achillea millefolium	-	0.0	45	3.8	25	4.0
Astragalus alpinus	-	0.0	-	0.0	90	16.0
Grasses						
Stipa lettermenii	-	0.0	45	6.8	50	3.8
Festuca idahoensis	-	0.0	40	6.5	50	4.5
Sedges						
Carex sp.	15	1.2	35	4.2	20	1.2
Rock	15	1.8	50	12.8	70	11.2
Bare soil	5	0.5	55	10.8	95	22.5
Litter	75	20.5	60	17.6	65	12.5
Total grasses	-	0.0	-	13.5	-	8.3
Total rock, soil, litter	-	22.8	-	41.2	-	46.2
Total vegetation	-	77.2	-	58.8	-	53.8

plants in each of the total exclusion and livestock exclusion parts of the exclosure. This was done to determine the effect of deer herbivory on that species.

Aspen in the total exclusion portion has regenerated since shortly after this exclosure was constructed and today is multi-sized and multi-aged despite the fact that the stand has been heavily invaded by conifers (Table 2), and is what the Forest Service would term a fast-seral aspen community (Mueggler 1988). Aspen has not been able to successfully regenerate in either the wildlife-only use area or the combined use area because all the aspen suckers have been repeatedly browsed by deer and/or domestic sheep (Table 2). When this site was measured in July, mule deer had already browsed many of the new aspen suckers inside the livestock exclusion part of the exclosure. The largest aspen stems were 30 cm DBH and 105± years old. Spruce overstory and understory canopy cover was greater on the grazed plots than the ungrazed portion of the exclosure (Tables 2 and 11).

Deer grazing and combined use also caused major differences in understory species composition. Deer grazing, as well as combined use, significantly ($p<.01$) reduced Indian paintbrush, dandelion, and total vegetative cover, while significantly ($p<.01$) increasing grass cover, yarrow (Achillea millefolium), and total rock, bare soil, and litter. Deer grazing also had a major effect on individual Indian paintbrush plants, significantly ($p<.01$) reducing mean height, mean crown diameter, and mean number of flower stalks (Table 12). When they were measured, deer had already grazed 63% of the Indian paintbrush flower stalks inside the livestock-exclusion portion of this exclosure. While I was at this site, I observed numerous humming birds feeding on

Table 11. Understory species composition inside and outside the Hancock exclosure.

	Mean percent canopy cover and frequency by treatment					
	Total exclusion		Livestock exclusion		Outside	
Species	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Trees						
Picea engelmannii	18	10.6	44	30.9	46	29.6
Shrubs						
Rosa woodsii	2	0.3	-	0.0	7	0.4
Forbs						
Castilleja miniata	56	29.5	6	0.4	2	0.2
Lupinus argenteus	37	14.2	50	8.8	34	7.7
Aquileja coerula	8	2.3	3	0.2	-	0.0
Traxacum officinale	29	4.6	-	0.0	-	0.0
Achillea millefolium	19	1.6	56	4.3	34	2.4
Aster sp.	13	2.4	9	0.9	9	0.7
Grasses						
Festuca thurberi	19	4.2	61	11.0	46	7.8
Bromus ciliatus	8	0.8	21	2.6	30	2.9
Rock	3	1.2	7	1.8	7	2.3
Bare soil	9	1.9	13	2.8	8	1.8
Litter	74	25.8	83	37.4	81	44.4
Total rock, soil, litter	-	28.9	-	42.0	-	48.5
Total rock, soil, litter plus *Picea*	-	49.5	-	72.9	-	78.1
Total grasses, forbs, and shrubs	-	50.5	-	27.1	-	22.9

Table 12: The effect of deer grazing on individual Castilleja miniata plants as measured inside the total exclusion and livestock exclusions portions of the Hancock exclosure.

Treatment	n	Mean height (cm)	Mean crown diameter (cm)	Mean number of flower stalks	Mean percent flower stalks grazed
Total exclusion* (no grazing)	25	58.6	51.9	19.3	0.0
Livestock exclusion* (deer only grazing)	25	36.0	21.8	7.3	62.8

*All means are statistically different at p=<0.01, Student's t test.

Indian paintbrush inside the total-exclusion area, but not inside the livestock exclusion area or on outside plots. Thus, grazing-induced reduction of this flowering forb may have had major effects on species not normally considered in range-wildlife studies.

Parker Mountain

The exclosure on Parker Mountain is the only five-part aspen exclosure encountered during this study (Table 1). Each of the two large total exclusion and livestock exclusion areas has been partitioned with additional fencing to prevent entry by lagomorphs on half of each respective exclosure. At the time this site was fenced, BLM thought that grazing by jackrabbits (Lepus spp.) might be having a negative effect on aspen regeneration. Thus, there are five parts to this exclosure - - all ungulates excluded, all ungulates plus lagomorphs excluded, livestock excluded, livestock and lagomorphs excluded, and unfenced outside areas. This exclosure was built around and through two decant aspen clones in 1974, and thus, has not been in place as long as the other exclosures measured during this study. Hence, the inside-outside differences may not be as great.

The exclosure is on a joint cattle-sheep allotment and mule deer have historically been abundant in this area, as have pronghorn antelope (Antilocapra americana). In recent years, however, the deer population has declined (see below) and most of the wildlife use on this site is now from elk, judging by the pellet groups that were present when the exclosure was measured in 1996. The enclosed aspen are also near the lower extent of aspen on this, the northeast end of Parker Mountain, and the site is

surrounded by sagebrush-grasslands. Thus, this is another ecotonal site at the lower distribution of aspen.

Nevertheless, when protected from all ungulates, aspen successfully regenerated producing a multi-aged stand (Tables 2 and 13). The total exclusion part of this exclosure was built through one aspen clone while the livestock exclusion part contains a small portion of the first clone plus it was also built through a second clone. To minimize clonal variation, the outside portion of both clones was sampled, which explains why the two outside data sets are slightly different (Tables 13-15). The exclusion or inclusion of lagomorphs had no significant influence on aspen regeneration (Table 13), so those data were combined to form a normal three-part exclosure (Table 2). Some aspen successfully regenerated in the livestock-exclusion part and on outside plots, especially after deer numbers declined (see below), but at significantly lower ($p<.05$) stem densities (Table 2). The increasing elk population, however, has now highlined those stems and inflicted extensive bark damage (Krebill 1972) on all the unprotected aspen. The largest aspen were 26-28 cm DBH and 90-95 years of age. Based on the distribution of new stems, aspen in the total exclusion part of this exclosure has spread into sagebrush-grasslands, an indication that climate is not limiting at this site.

Although this exclosure had been in place for only 22 years, there were still significant ($p<.05$) differences in understory species composition (Tables 14 and 15). The palatable forbs Castilleja linariaefolia and Penstemon procerus had greater canopy cover in the total exclusion part, while their abundance was reduced by wildlife use, and virtually eliminated by combined wildlife-livestock use. Conversely, native grasses were

Table 13. Aspen stem densities by size classes inside and outside the Parker Mountain exclosure.

Treatment	Sample size*	Mean aspen stem density by size classes (stems/ha)**				
		2m	2m-5cm	6-10cm	11-20cm	>20cm
All ungulates excluded	4	1,127	3,173	1,670	125	459
All ungulates plus lagomorphs excluded	2	668	1,670	584	0	584
Outside	3	835	56	0	0	557
Total all ungulates excluded	6	974	2,672	1,308	84	500
Livestock excluded	3	5,177	223	0	0	111
Livestock plus lagomorphs excluded	3	3,841	557	0	0	56
Outside	3	1,225	0	0	0	56
Total livestock excluded	6	4,509	389	0	0	84

* Sample size = the number of 2x30m transects used to count aspen stems and to measure understory species composition.

** Aspen stem size classes: 2m = stems less than 2m tall; 2m-5cm = stems greater than 2m tall but 5cm or less diameter at breast height (DBH); 6-10cm = stems 6-10cm DBH; 11-20 cm = stems 11-20cm DBH; and >20cm = stems greater than 20cm DBH.

Table 14. Understory species composition inside and outside the total exclusion portion of the Parker Mountain exclosure.

Species	Mean percent canopy cover and frequency by treatment							
	Total exclusion		Total exclusion + lagomorphs		Combined total exclusion		Outside	
	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs								
Artemisia tridentata	31	15.2	42	16.3	35	15.6	51	21.1
Symphoricarpos oreohilus	3	2.5	-	0.0	2	1.7	-	0.0
Grasses								
Sitanion hystrix	31	4.8	55	9.5	39	6.4	31	2.7
Stipa comata	21	3.2	25	3.0	22	3.1	19	1.5
Stipa columbiana	3	0.6	8	4.1	4	1.8	-	0.0
Agropyron caninum		0.4	-	0.0	2	0.3	19	1.2
Koeleria cristata	6	0.8	-	0.0	4	0.5	-	0.0
Festuca thurberi	59	25.0	61	17.4	60	22.5	77	8.7
Poa interior	7	0.7	7	1.8	7	1.1	19	1.5
Bromus ciliatus	44	15.5	67	11.5	52	14.2	14	1.3
Poa pratensis	19	5.6	-	0.0	13	3.7	6	0.6
Forbs								
Castilleja linariaefolia	14	2.8	5	1.0	11	2.2	-	0.0
Penstemon procerus	8	1.1	38	9.0	18	3.7	-	0.0
Rock	-	0.0	-	0.0	-	0.0	-	0.0
Bare soil	2	0.3	2	0.7	2	0.4	37	12.9
Litter	66	21.6	77	25.3	70	22.8	81	48.1
Total grasses	-	56.6	-	47.3	-	53.6	-	17.5
Total forbs	-	3.9	-	10.0	-	5.9	-	0.0
Total vegetation	-	78.1	-	74.0	-	76.8	-	39.0

Table 15. Understory species composition inside and outside the livestock exclusion portion of the Parker Mountain exclosure.

Species	Mean percent canopy cover and frequency by treatment							
	Livestock exclusion		Livestock exclusion + lagomorphs		Combined livestock exclusion		Outside	
	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover	Frequency	Canopy cover
Shrubs								
Artemisia tridentata	63	40.1	51	31.7	57	35.9	59	40.1
Symphori	-	0.0	-	0.0	-	0.0	10	5.8
Grasses								
Sitanion hystrix	28	4.4	17	2.1	22	3.2	12	1.1
Stipa comata	23	3.3	18	2.1	20	2.7	12	1.3
Koeleria cristata	40	4.3	30	4.2	35	4.2	47	5.2
Festuca thurberi	4	0.7	-	0.0	2	0.4	-	0.0
Festuca idahoensis	61	11.7	63	15.5	62	13.6	57	7.1
Bromus ciliatus	2	0.2	-	0.0	1	0.1	-	0.0
Forbs								
Castilleja linariaefolia	6	0.5	19	2.5	12	1.5	1	0.1
Phlox sp.	19	3.9	23	4.7	22	4.3	13	2.3
Rock	36	8.1	13	3.3	24	11.4	13	2.8
Bare soil	31	5.1	16	3.2	24	4.2	40	15.9
Litter	60	17.8	72	30.8	66	24.3	52	19.4
Total grasses	-	24.6	-	23.9	-	24.2	-	14.7
Total forbs	-	4.4	-	7.2	-	5.8	-	2.4
Total vegetation	-	69.1	-	62.8	-	66.0	-	63.0

most abundant in the total exclusion part (54%), but that value was halved by wildlife use (primarily elk, as elk normally consumes more grasses than mule deer), and reduced to a mean of 16% under combined use. Livestock grazing also significantly ($p.<.05$) increased the amount of bare soil.

DISCUSSION

Aspen Stem Dynamics

Aspen within all total exclusion treatments successfully regenerated without disturbance and developed multi-sized, multi-aged stems even where the stand had been heavily invaded by conifers (i.e., the Hancock exclosure). Aspen subjected to browsing only by wildlife, primarily mule deer, either failed to produce new stems greater than 2 m tall, or regenerated at stem densities significantly lower than that on total exclusion plots. While on combined wildlife-livestock use plots, most aspen failed to successfully regenerate, or did so at even lower stem densities. Moreover, aspen successfully regenerated on livestock exclusion and combined use plots only when mule deer populations were low.

Mule deer numbers in Utah peaked during the early 1960s, but declined precipitously by 1975 due, primarily, to overhunting of females (Workman and Low 1976, Short 1979 - - see Figure 4). This reduced the browsing pressure on aspen suckers and many stands in southern Utah were able to successfully regenerate, especially where livestock use was not excessive (Figure 5). When mule deer numbers rebounded during the 1980s, however, those animals not only prevented new aspen suckers from increasing in height, but they also consumed all the lower branches from the aspen that had successfully regenerated earlier (Figure 5). By the mid-1990s, mule deer populations had again declined to relatively low numbers, but few aspen stands were able to successfully regenerate, because elk numbers had risen more than 10-fold since the 1960s. That is to say, deer overbrowsing has been replaced by elk

Figure 4. The number of mule deer and elk harvested by hunters in Utah from 1925 to 1995. Elk and mule deer were rare when Utah was first settled by Europeans (Rawley 1985), as was true throughout the Intermountain West (Kay 1994, 1995, 1997a). With the advent of modern game management, however, mule deer numbers increased dramatically from 1925 to 1960, while elk populations were purposely kept low to avoid conflicts with livestock and private ranchlands. Only after a change in management around 1965 were Utah's elk herds allowed to expand. Nevertheless, elk numbers are still significantly less than those of mule deer. Data from Utah Division of Wildlife Resources' Annual Big Game Reports were smoothed to show historical trends. Graphed are the total harvests for both sexes for each species. From 1940 to 1975, the number of domestic sheep in Utah fell from over 2 million to around 500,000, while cattle numbers increased from less than 300,000 to over 700,000 (Workman and Low 1976:27).

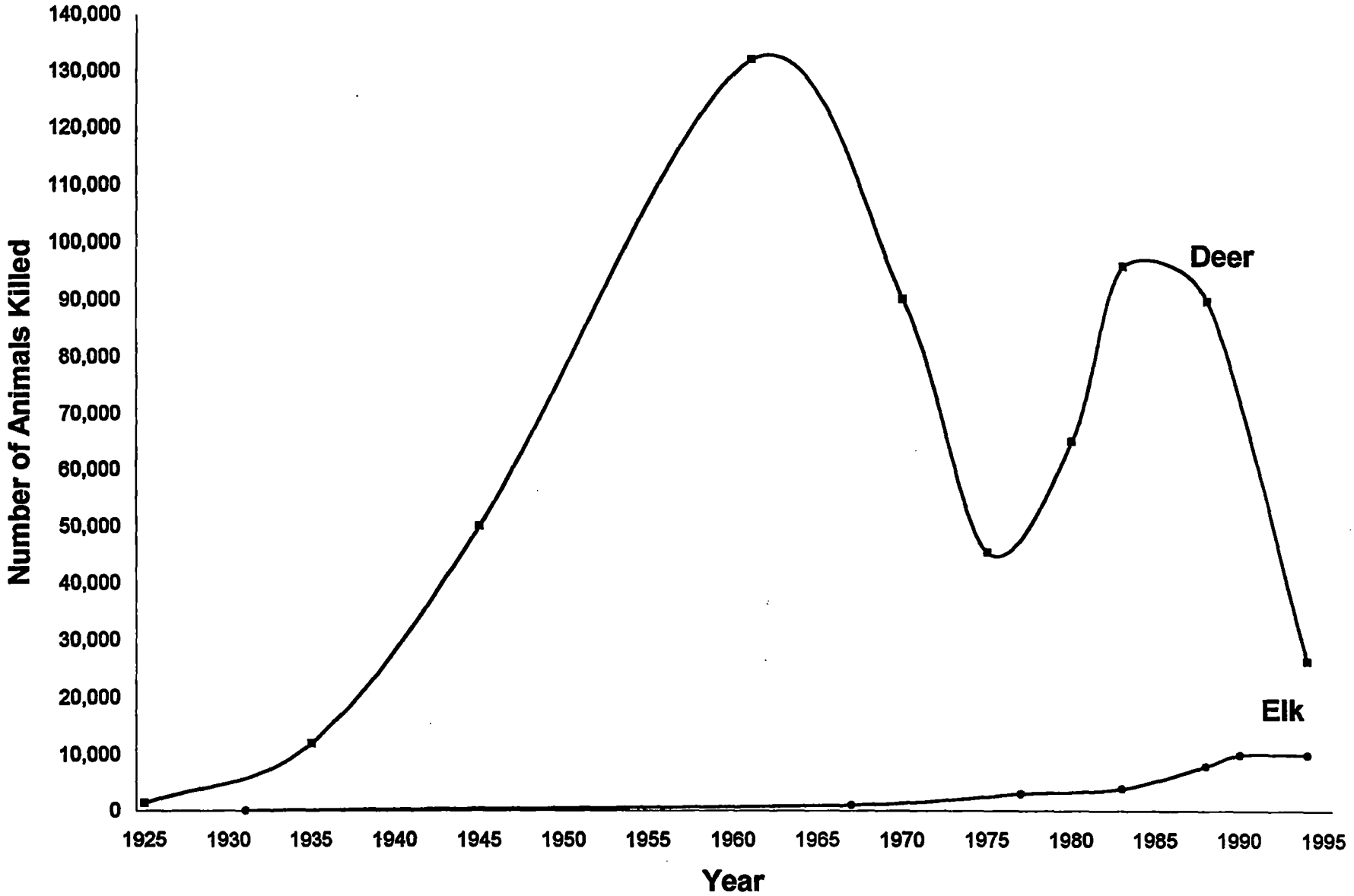

Number of Animals Killed
140,000
130,000
120,000
110,000
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1925
1930
1935
1940
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
Year
Deer
Elk

Figure 5. High-lining of aspen on the Dixie National Forest by mule deer. When deer numbers were low during the mid to late 1970s, browsing pressure was reduced, and some aspen stands were able to produce new stems greater than 2 m tall, without fire or other disturbance. As deer numbers rebounded during the mid to late 1980s, however, those animals then consumed the lower branches of the newly regenerated aspen, as high as the mule deer could reach - - termed high-lining. Recent, combined deer and cattle use has also prevented any new suckers from reaching more than 1 m in height. Print from color slide taken near Blue Grass Lake on the southeast slope of Boulder Mountain by Charles E. Kay on October 7, 1991.

Figure 5

overbrowsing in many areas of Utah. Elk also seem to have a greater preference for aspen than do mule deer (Kay 1990, 1997a, 1997c; Shepperd and Fairweather 1994). Alder (1970), Julander and Low (1976), and Olmstead (1974) all reported other episodes of aspen regeneration when mule deer numbers were low, while Olmstead (1977, 1979), Kay (1990), and Kay and White (1995) reported an identical pattern with elk.

Understory Species Composition

Ungulate herbivory also had significant effects on the understory species composition of aspen stands. In general, utilization by mule deer tended to eliminate shrubs and tall, palatable forbs while favoring the growth of native grasses and unpalatable forbs. Indian paintbrush, in particular, was severely impacted by mule deer herbivory. With the addition of livestock use, primarily cattle, native grass cover was significantly reduced at most sites, while non-native grasses and bare soil increased. It is clear that the combined level of ungulate use that has occurred and is occurring at all sites has had and is having a negative impact not only on aspen stem dynamics, but understory species composition, as well. It is equally clear, however, that wildlife use alone has and is dramatically effecting aspen community structure. Earlier open-range grazing studies reported similar results (Sampson 1919, Baker 1925, Coles 1965, Weatherill and Keith 1969, Alder 1970, Julander and Low 1976, Mueggler 1988; but see Smith et al. 1972).

Other Aspen Exclosure Studies

Mueggler and Bartos (1977) reported that shrubs increased inside two, three-part aspen exclosures (Grindstone and Big Flat) in southern Utah where mule deer and cattle were the primary ungulate herbivores. They concluded that,

> ... the most striking difference in understory attributable to animal use was the great reduction in total shrubs ... After 41 years, the ungrazed area at Grindstone Flat produced almost 10 times more shrubs than the area grazed by both cattle and deer and over three times more than that grazed just by deer. The graminoids increased under grazing at Grindstone Flat ... [p. 13].

Aspen protected from all grazing developed multi-size-class stands while those outside did not.

Coles (1965:38-41) measured the age structure of aspen communities inside and outside a three-part exclosure in central Utah. Where all ungulates were excluded, aspen stems were multi-aged. Where cattle were excluded but mule deer were not, few new stems had grown taller than 2 m. However, "Damage to aspen reproduction was even greater on the open plot grazed by both deer and cattle" (Coles 1965:40). Not only did cattle consume some of the aspen, but "an indirect effect of cattle grazing appeared to be the destruction of desirable game forage which forced game to utilize aspen [more heavily]" (Coles 1965:56).

Trottier and Fehr (1982:28-33) reported on an aspen exclosure in Canada's Banff National Park where elk were the most abundant ungulate. They (p. 28) noted that "Browsing by elk in this area has a tremendous influence on shrub and tree regeneration in the aspen forest." The protected plot had greater shrub density and a more diverse height class distribution than the browsed plot. "About 97% of the shrubs

in the browsed plot were less than 100cm high and there were no plants taller than 150cm" (p. 30). The authors (p. 30) concluded that aspen regeneration was limited by ungulate browsing. "Under protection there were plants [aspen] in all height classes indicating that growth to tree stage was proceeding. On the browsed plot all plants were less than 100cm" (p. 30).

When Banff's aspen exclosure was erected in 1944, two photopoints were established. One inside the protected area and another immediately outside. Retakes 50 years later showed that a dense multi-aged aspen stand had grown-up inside the exclosure, while no aspen stems had successfully regenerated on outside plots (Kay et al. 1994). Kay et al. (1994) also reported on aspen that had been protected for approximately 10 years within the game-proof fenced Trans Canada Highway right-of-way through Banff's lower Bow Valley. Where elk were excluded, aspen had successfully regenerated, while there was no response on grazed plots.

Milner (1977) measured aspen communities inside and outside four exclosures in Alberta's Elk Island National Park where elk and moose are the major ungulates. Inside each exclosure, aspen "attained a greater basal area, height and DBH class" than on outside plots (p. 52). Moreover, "Regeneration of the tree structure was restricted in unprotected areas ... [and] shrub height and diameter class were greater in the exclosures" (pp. 52-53). Highly palatable shrubs increased significantly inside the exclosures. That is to say, ungulate browsing prevented aspen regeneration and favored grasses over shrubs.

Gysel (1960), Olmsted (1977), Hart (1986), Stevens (1980), Hess (1993), and Baker et al. (1997) reported on aspen enclosures in Colorado's Rocky Mountain

National Park where elk and mule deer are the primary ungulates. In three out of four enclosures, aspen developed multi-aged stands while those outside did not. In the fourth, aspen was completely replaced by conifers (Hart 1986), but conifers did not establish in the other enclosures (Olmsted 1977:27). Inside the three enclosures, aspen spread into and replaced grasslands while outside, grazing changed aspen communities into grasslands (Gysel 1960, Stevens 1980, Hart 1986). Shrubs were more common inside the enclosures than out (Stevens 1980). A temporary reduction of elk numbers inside the park allowed some aspen stems to escape browsing and to grow into larger size classes (Olmstead 1977, 1979).

Kay (1990:84-122) measured 14 aspen containing exclosures in the Yellowstone Ecosystem where elk are the major ungulate herbivore. At no sites were livestock permitted. He found that all aspen stands protected from wildlife successfully regenerated and developed multi-age structures. He also found that repeated elk use had completely changed understory plant communities. Inside exclosures, shrubs and palatable forbs dominated, while grasses were a minor component. Conversely outside exclosures, aspen understories were dominated by non-native grasses resistant to grazing, while shrubs and palatable forbs were rare. In the absence of grazing, Yellowstone's aspen exhibited multi-age structures and understory species compositions of climax communities (Mueggler 1988), while outside the exclosures, aspen displayed all the characteristics of grazing disclimaxes and retrogressive plant succession. Moreover, few exclosures had been invaded by conifers.

In South Dakota's Custer State Park, aspen expanded into and replaced grasslands inside an exclosure within 2 years following exclusion of wildlife grazing

(Hoffman and Alexander 1987:15). While at South Dakota's Wind Cave National Park, aspen inside an exclosure developed into a multi-size class stand while those subject to wild ungulate use did not (Kay 1990:115). Similarly, Herlburt and Bedunah (1996:23) measured three-part aspen-containing exclosures in north-central Montana and reported that "grazing solely by wild ungulates [mule deer and elk] dramatically influenced ... aspen communities." Moreover, elk and deer tended to eliminate shrubs, while cattle use favored non-native grasses.

Thus, aspen exclosure studies throughout the western United States and Canada support the results reported here. Namely that deer and elk use alone can have a significant effect on aspen regeneration and understory species composition. Moreover, livestock use has an additive negative impact on aspen regeneration and further changes understory species composition. Again, wildlife use tends to eliminate woody species and palatable forbs. While utilization by mule deer favors native grasses, elk use has a negative impact on grassland communities due to the latter ungulate's wider diet breadth (Nelson and Leege 1982). Cattle grazing also tends to eliminate native grasses while significantly increasing non-native species and bare soil.

Climate Change

Exclosures also demonstrate that climatic variation has had little effect on aspen communities compared to that imposed by ungulates. Since the climate is the same on both inside and outside plots, its influence is constant. The more profuse vegetation inside the exclosures, and especially on total exclusion plots, itself alters the

microclimate, but that is an incorporated variable caused by the plants' response to the elimination of ungulate browsing, not the cause of the vegetation's response. Such microclimatic conditions would prevail in any aspen stand not subject to heavy ungulate use, whether in an exclosure or not.

Furthermore, if climatic variation was having an overriding effect on aspen community dynamics as proposed by others (Romme et al. 1995), then it would be logical to expect aspen inside exclosures in south-central Utah to be showing signs of physiological stress, especially since many of the exclosures are situated at the lower distributions of aspen or at grassland-aspen ecotones. No signs of physiological stress, however, were observed during the course of this study. In fact, as noted above and as depicted in Figures 2 and 3, the area occupied by aspen has increased inside exclosures at the expense of grasslands. That is to say, protected aspen communities grew into and displaced dry grasslands, something that would not be expected if a warming, drying climate was adversely impacting aspen. Baker et al. (1997) also reported no correlation between climatic variation and aspen regeneration, while Kay (1990:119-122) reported that enclosed aspen in the Yellowstone Ecosystem replaced grasslands even on south-facing hillsides. Similarly, White et al. (1997) and Kay (1997c) reported no correlation between climate and aspen regenerations in the Canadian Rockies.

CONCLUSIONS

1. Ungulate herbivory has prevented and is preventing aspen regeneration throughout south-central Utah.
2. Aspen need not be burned or clear-cut to successfully regenerate. Even stands heavily invaded by conifers will successfully regenerate if ungulate use is at or below per-1870 levels.
3. Wild ungulates, primarily mule deer, have had a major impact on aspen stem dynamics and understory species composition.
4. Livestock use has also had widespread impacts on aspen communities, including understory species composition.
5. Combined wildlife-livestock use has been even more damaging to aspen communities.
6. By changing aspen stem dynamics and understory species composition, ungulate herbivory has likely also had negative impacts on birds, small mammals, and total biodiversity.
7. Aspen stands dominated by old-age or single-age trees are not a biological attribute of aspen, but an artifact of excessive ungulate browsing.
8. Managers should quantify the level of ungulate herbivory before treating aspen stands with fire or by cutting, because once the overstory trees are killed, all the remaining sprouts are subject to repeated browsing. In fact, if ungulate herbivory is excessive, treating aspen stands will only hasten their demise (Kay 1997a, 1997b, 1997c). While Mueggler and Bartos (1977) and Smith et al. (1972) reported that treating large areas of aspen at one time may swamp ungulate

herbivores and allow aspen to successfully regenerate, recent evidence has not supported those observations. In Yellowstone, for instance, the 1988 wildfires burned approximately one-third of the aspen on the park's northern range, yet elk herbivory not only prevented successful aspen regeneration (Romme et al. 1995), but also led to the elimination of many aspen clones (Kay and Wagner 1996; Kay unpub data). Moreover, Banff National Park recently suspended its prescribed burning program until elk herbivory can be controlled (Page et al. 1996a, 1996b), while an independent panel recommended that Rocky Mountain National Park not burn any of its aspen communities unless ungulate herbivory is first controlled (Berry et al. 1997)

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